

## MOTION PERCEPTION CORRELATES WITH VOLITIONAL BUT NOT REFLEXIVE EYE MOVEMENTS

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**Abstract**—Visually-driven actions and perception are traditionally ascribed to the dorsal and ventral visual streams of the cortical processing hierarchy. However, motion perception and the control of tracking eye movements both depend on sensory motion analysis by neurons in the dorsal stream, suggesting that the same sensory circuits may underlie both action and perception. Previous studies have suggested that multiple sensory modules may be responsible for the perception of low- and high-level motion, or the detection versus identification of motion direction. However, it remains unclear whether the sensory processing systems that contribute to direction perception and the control of eye movements have the same neuronal constraints. To address this, we examined inter-individual variability across 36 observers, using two tasks that simultaneously assessed the precision of eye movements and direction perception: in the smooth pursuit task, observers volitionally tracked a small moving target and reported its direction; in the ocular following task, observers reflexively tracked a large moving stimulus and reported its direction. We determined perceptual–oculomotor correlations across observers, defined as the correlation between each observer's mean perceptual precision and mean oculomotor precision. Across observers, we found that: (i) mean perceptual precision was correlated between the two tasks; (ii) mean oculomotor precision was correlated between the tasks, and (iii) oculomotor and perceptual precision were correlated for volitional smooth pursuit, but not reflexive ocular following. Collectively, these results demonstrate that sensory circuits with common neuronal constraints subserve motion perception and volitional, but not reflexive eye movements. Crown Copyright © 2014 Published by Elsevier Ltd. on behalf of IBRO. All rights reserved.

**Key words:** smooth pursuit, ocular following, individual differences, direction, perception.

### INTRODUCTION

Visual processing in the brain subserves two related purposes: guiding actions and informing perception. In

the visual cortical hierarchy, these roles are often separately ascribed to the dorsal and ventral streams, respectively (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). Motion processing provides an excellent system for examining links between action and perception within a single stream, as it is traditionally associated with sensory processing by dorsal-stream neurons in the middle temporal area (MT) and medial superior temporal area (MST) (Born and Bradley, 2005). It is well established that MT/MST neurons drive volitional smooth pursuit (SP) eye movements (Komatsu and Wurtz, 1989), reflexive ocular following (OF) eye movements (Kawano et al., 1994; Ibbotson et al., 2007), and motion perception (Newsome and Pare, 1988; Britten et al., 1996). However, it remains unclear whether motion perception and the control of eye movements have overlapping computational constraints, and whether overlapping circuits control volitional and reflexive movements.

If motion perception and eye movements depend on shared sensory processing, errors in an observer's perceptual and oculomotor performance might be correlated across trials. Such correlations have been reported between SP and direction perception (Krauzlis and Adler, 2001; Stone and Krauzlis, 2003), but not for tasks requiring speed judgments during pursuit (Gegenfurtner et al., 2003; Tavassoli and Ringach, 2010), or during OF (Bostrom and Warzecha, 2010; Spering et al., 2011; Blum and Price, 2014; Glasser and Tadin, 2014). The presence of correlations in only some studies is attributable to a range of causes, including: (1) noise downstream from the region of common processing overwhelming any measurable correlation; (2) perceptual task differences (e.g. direction versus speed judgments); (3) oculomotor task differences (e.g. reflexive versus volitional movements); (4) efference copy modifying sensory processing; and (5) eye movements impairing perception (Schutz et al., 2011; Spering and Montagnini, 2011). Any of these conditions would make it more difficult to observe correlated variability between two tasks, even when those tasks depend on common sensory neurons.

One way to overcome these limitations is to compare variability across *observers*, rather than across *trials* performed by a single observer. Individual differences studies have demonstrated that an observer's performance on one perceptual task can predict their performance “within-domains” on other perceptual tasks, and “between-domains” on motor tasks (Wilmer and Nakayama, 2007; Wilmer, 2008). These results are

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**Abbreviations:** CRT, cathode ray tube; hMT+, human motion complex; LCD, liquid-crystal display; MST, medial superior temporal area; MT, middle temporal area; OF, ocular following; RDC, random dot cinematograms; SP, smooth pursuit.

interpreted as evidence that the same neural circuit, or neural systems with common processing constraints, are involved in each task (Halpern et al., 1999; Kosslyn et al., 2002; Wilmer, 2008).

We compared the precision of motor responses (SP and OF) and direction perception. We primarily assessed perceptual–oculomotor correlations, defined as the across-observers correlation between each observer's mean perceptual precision and mean oculomotor precision. We show that performance on perceptual and *volitional* behavioral tasks is correlated, whereas performance on perceptual and *reflexive* behavioral tasks is not correlated. While different requirements for the spatial integration of motion may account for the differences between OF and pursuit, our results suggest that sensory circuits with common neural constraints perform the motion analysis for action and perception.

## EXPERIMENTAL PROCEDURES

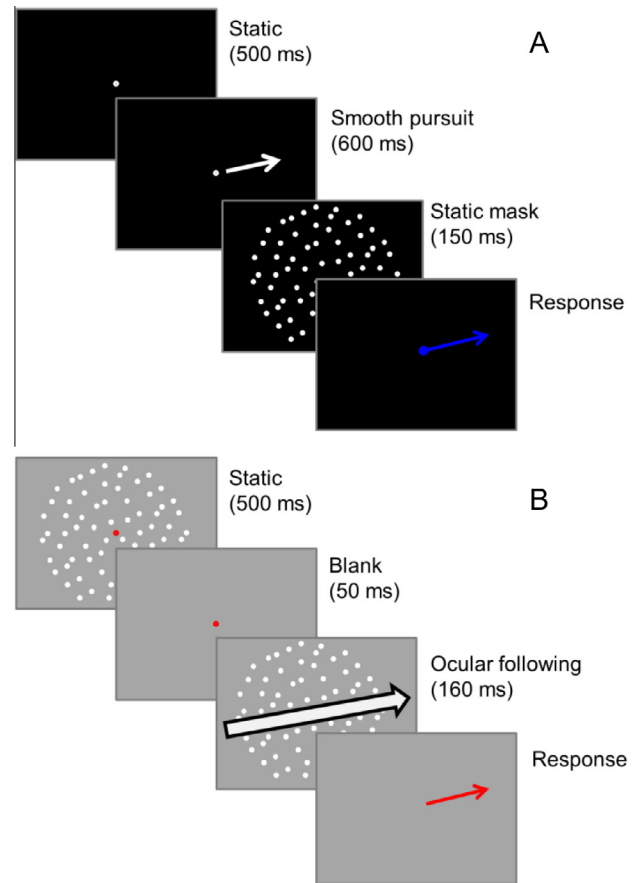
### Participants

Thirty-nine volunteers (21 females, 18 males; ages 18–65) with normal or corrected to normal vision participated in the experiment. All had no, or limited, prior psychophysical experience. Fifteen observers participated as part of an undergraduate project and the remainder were compensated for their time. Before data collection commenced all observers completed ~20 trials of each task to familiarize themselves with the stimulus and methods. Data from three participants were excluded due to the participants' inability to correctly track a target during the SP task. All procedures were approved by the Monash Human Research Ethics Committee and volunteers gave informed written consent.

### Apparatus

Participants were comfortably seated facing a  $52.5 \times 29.5$ -cm liquid-crystal display (LCD) monitor (VIEWPixx; 120 Hz refresh rate;  $1920 \times 1200$  pixels). Four participants were tested for a single session using a  $34.8 \times 30$ -cm cathode ray tube (CRT) monitor (IBM 6558 P202; 100 Hz refresh rate;  $1280 \times 1024$  pixels) and we observed no qualitative differences between their results with the LCD or CRT monitor. A chin and forehead rest was used to stabilize the head and maintain a viewing distance of 65–74 cm. Stimuli were generated using Matlab (The Mathworks, Natick, MA, USA) and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

Eye movements were recorded using a non-invasive infrared eye-tracker with a sampling resolution of 1000 Hz (Eyelink 1000, SR Research, Ottawa, Canada). A 5-point calibration procedure for the eye tracker was repeated every 20–24 trials and also if participants did not fixate at the start of a trial within 5 s of the appearance of the fixation spot. To minimize eye tracker signal loss, participants were encouraged to blink between, rather than during, trials.



**Fig. 1.** Stimuli and tasks. (A) In the smooth pursuit task, participants fixated a central stationary white target. At a random time, the target was displaced by  $1.5^\circ$  in one of twelve randomly selected directions and immediately began moving at 10-deg/s toward, and then past, its original position. After 600 ms, the target disappeared and was replaced by a static mask, comprising stationary, but flickering dots. Participants were given a 10-s window in which they used a computer mouse to drag an arrow to indicate the target direction. (B) In the ocular following task, participants fixated a central red spot in a field of stationary, flickering dots for 500 ms. Following a blank period, the dot field reappeared and all dots moved at 16-deg/s with 90% coherence in the same direction. Participants indicate their perceived motion direction in the same way as for the pursuit task. In all subsequent figures, pursuit and ocular following data are blue and red, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### SP stimulus

An individual SP trial consisted of four stages (Fig. 1A): fixation of a static target for 500 ms; SP tracking for 600 ms, in which the target jumped 1.5 deg and immediately began moving toward and then past its initial location at 10-deg/s; a static mask for 150 ms, to decrease the probability of an after-image or memory of the final target position influencing perceptual responses; and a response period limited to 10 s. The target was a single white spot with radius 0.4 deg and luminance  $100 \text{ cd/m}^2$  moving on a black background ( $0.3 \text{ cd/m}^2$ ). The backward 1.5-deg step allowed observers to immediately begin smooth tracking of the target, without a catch-up saccade. The mask contained stationary white dots of the same radius and luminance

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